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by Richard L. Knight

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Since time immemorial humans have lived and subsisted in wilderness areas. Perhaps it is not surprising then that once human dependency on wilderness for subsistence was removed, humans continued to seek out wildlands for other needs (Nash 1967). Increasingly, humans in industrialized societies have turned towards sparsely settled lands for relief from their more congested urban homes. The values they seek vary but recreation is a high priority.

Traditionally, the major types of recreational activities in wilderness areas involved some form of consumptive use, chiefly hunting or fishing. Beginning in the 1960's, and accelerating rapidly to the present, recreation types have broadened. Today, one is more likely to see backpackers, mountaineers, or nature photographers when venturing into wildlands (Hammitt and Cole 1987).

The result has been a "recreational boom" in the use of wildlands, and today, resource managers are faced with a new suite of responsibilities. Traditionally their duties were concerned mostly with monitoring the removal of natural resources from the land. This included mining, logging, grazing, and hunting and fishing. With the changes in human demographics, and resultant legislative decrees, natural resource agencies, such as the United States Forest Service, increasingly find themselves responsible for enhancing recreational opportunities. As an example, the sharp increase in backpacking, and the resultant multi-million dollar industry it has generated, has created a strong demand for hiking trails and back country campsites.

With this "recreation boom" has come the recognition that wilderness and recreational activities are not compatible without some form of management (Hammitt and Cole 1987). Although wilderness management is in its infancy, a brief review of its progression is warranted. Initially, managers were concerned with simply the number of people using an area. This led to the use of permits to control party size and numbers of parties. Next, attention was turned to the impacts of wilderness users on vegetation and water quality. This resulted in spatial and temporal restrictions around campsites, trails, and riparian areas. The next area of interest focused on the effects of recreational activities on wildlife (Schoenfeld and Hendee 1978, Peek 1986:409-416). This need arose because of legislation concerning wildlife (e.g., The Endangered Species Act) and the recognition that wildlife viewing was a recreational activity in its own right. As in the previous two stages, understanding in this arena will come only with carefully conducted research followed by field application of the results and careful evaluation by managers (Knight and Knight Skagen 1988).

In this document I focus on the effects of recreation on wildlife in wildlands. My goal is to review and summarize the literature on this topic and highlight generalizations and contradictions that exist. Specifically, I will attempt to address the following questions: What criteria can be used to assess the effects of recreationists on wildlife? What effects do different recreational activities have on wildlife? What influences the responses of wildlife to recreational activities? What is the magnitude of the wildlife response to these activities? What are the proximate and ultimate factors explaining these responses? What management options exist which allow wildlife and recreationists to coexist? What needs to be known to improve the management of wildlife in wilderness areas?

Because there is so little empirical information available regarding these questions, I have searched a larger pool of knowledge. I included studies that looked at the effects of recreation on wildlife, regardless of the setting (e.g., cities, rural areas). I have also used those studies that have measured the responses of wildlife to research investigators. Finally, I searched the behavior literature in order to understand aspects of animal learning.

ASSESSING THE EFFECTS OF RECREATIONISTS ON WILDLIFE

There are two areas in the field of recreation/wildlife management where objective criteria are needed to assess wildlife responses. A similar set of criteria is sufficient for both needs.

First, natural resource managers require criteria to determine if recreationists are affecting wildlife. That human activity is ubiquitous in most landscapes is now widely accepted yet our understanding of its effects on wildlife populations and communities is poor (Boyle and Samson 1985). In spite of this, applied ecologists work within the paradigm that human activities (e.g., recreational activities) negatively impact wildlife. It is overly simplistic to assume that all activity has the same effect, and that the effect is always negative. For natural resource managers to critically evaluate effects of recreationists on wildlife there will need to be objective criteria to evaluate these types of activities (Pomerantz et al. 1988).

Second, natural resource managers need criteria to evaluate the effects of management programs designed to minimize undesirable effects of recreationists on wildlife. For example, a goal of a National Forest might be to insure intact cliff-using wildlife communities, in spite of a heavy demand by rock climbers to utilize these cliffs. Forest personnel might enact a management program that would spatially and temporally isolate climbers from critical sections of cliff.

In order to determine whether these actions met their management goal, criteria would be necessary to see whether isolating rock climbers spatially or temporally from cliff-using wildlife minimized the negative impacts on the wildlife community.

Surprisingly, criteria to evaluate the impacts of human activities on wildlife has received scant attention. The most complete effort to date has been by Pomerantz et al. (1988). They developed a classification of 6 non-mutually exclusive categories of negative impacts that recreational activities may have on wildlife (Table 1). I have modified this scheme to reflect a more neutral human orientation and to encompass wildlife communities and populations rather than just individuals (Table 2).

One important aspect of this classification scheme is that it encompasses the full spectrum of responses that recreationists may have on wildlife. It has been a tacit assumption that human disturbance is detrimental to wildlife individuals and populations, although disturbance has rarely been linked to changes in reproduction, survival or any other demographic parameters. Indeed most empirical studies on recreation/wildlife interactions have looked only at the behavioral responses of wildlife. These authors then make a leap of faith that since wildlife reacts to their presence this will negatively impact the species. The scheme in Table 2 allows for wildlife responses as subtle as flushing to an intruder, to the disruption of an entire wildlife community.

WILDLIFE RESPONSES TO DIFFERENT TYPES OF RECREATIONAL ACTIVITIES

In this section I examine types of recreational activities and examine whether they effect wildlife according to the criteria listed in Table 2. Because there is a scarcity of wildlife/recreation/wilderness studies, I also included studies from sites other than true wilderness areas.

Several generalizations emerge from an examination of this literature. First, most field studies have restricted their response variables to behavioral reactions of wildlife to the disturbance. Few researchers have addressed whether survival or population changes occur. Secondly, several popular recreation activities in wildlands have received little attention. For example, only three published studies have examined the effects of cross-country skiing on wildlife; there were none pertaining to downhill skiing. Third, recreationists negatively affect wildlife at the individual, population, and community level. These findings agree with those of Boyle and Samson (1985) who reported that 81% of 166 articles that contained original data on effects of nonconsumptive outdoor recreation on wildlife in North America found evidence of negative effects on wildlife. It appears, therefore, that the tacit assumption that recreation negatively impacts wildlife is supported.

A caveat that requires consideration is what is meant by "negative" or "positive" effects? Rightly or wrongly, it appears that this is largely an anthropocentricly-determined value. For example, recreationists might cause an increase in a species' survival rate (e.g., by supplemental feeding) to the point where its numbers increase. If this species, because of its increased numbers, then became a pest to humans would this then be considered a positive or negative effect? Raccoons (Procyon lotor) that feed on human food wastes in campgrounds may have an increased survival rate which results in a population increase. Alternatively, more raccoons may simply concentrate in the vicinity of campgrounds to feed on the readily available food. In either case, recreationists have altered the number of raccoons and their behavior. At some point natural resource personnel may decide that raccoons at campgrounds are a pest species. Initially, recreationists would have had a positive effect (i.e.,

population increase) which would in time be viewed negatively and result in a negative effect (i.e., designation of raccoons as a pest species and resultant control).

The caveat, therefore, is that "positive" or "negative" is defined by the natural resource manager. One could expand this value-making authority to include citizen-user groups (e.g., The Wilderness Society). In both cases these terms are value-loaded and refer to what is good or bad for humans, not necessarily wildlife.

When considering the effects of recreational activities on wildlife, it must be appreciated that not all types of activity have different impacts. For example, the presence of a bird watcher along a shoreline may have the same effect as an angler. In addition, recreational activities must not be viewed in isolation. There may be synergisms or interactions when more than one recreational activity is occurring simultaneously. For example, at a reservoir in South Wales sailing was not viewed as detrimental to waterfowl because it occurred in deep waters and waterfowl preferred the shallows. However, when bank fishing occurred waterfowl retreated to the deeper central waters where they encountered sailors. Angling and sailing, therefore, resulted in birds being deprived of any part of the reservoir (Bell and Austin 1985). Finally, not all types of recreational activities in wildlands are necessarily dependent upon wildlife. Activities such as nature watching and hunting, are closely associated with areas of high wildlife diversity, whereas, activities, such as hiking, may not be.

Types of recreational activities

Backpacking/hiking/cross-country skiing/horseback riding: These activities all involve human beings traveling by means of non-motorized vehicles in

wildlands. Likewise, they have all increased in popularity which in turn has caused the creation of many more miles of hiking, skiing, and riding trails penetrating wildlands. They all have the ability to disrupt wildlife, chiefly through redistribution of animals, and alteration of behavior.

One of the most conspicuous responses of ungulates to wilderness travelers is the displacement of individuals from used areas. Hamr (1988) found that hiking and skiing activities displaced chamois (*Rupicapra rupicapra*) from nutritionally important habitats for prolonged periods. Roe (*Capreolus capreolus*) and red deer (*Cervus elephus*) in Denmark were displaced by orienteering activities, yet the animals usually returned within 4 days after cessation of the disturbances (Jeppesen 1987a, Jeppesen 1987b). Hicks and Elder (1979) reported that bighorn sheep (*Ovis canadensis*) avoided meadows frequented by hikers and mountaineers. This difference, however, was attributed to vegetative differences. Backpackers and bighorns were able to coexist due to spatial differences in habitat use; backpackers used trails and camped near water, whereas, bighorns used areas where these features did not exist.

A study which compared the breeding success of red grouse (*Lagopus lagopus*) on two moors in the Peak District National Park, England, showed that grouse bred no worse on moors where people had unrestricted access and than on moors where hikers were restricted to rights-of-ways (Picozzi 1971). Swenson (1979) studied factors influencing reproductive success among ospreys (*Pandion haliaetus*) nesting in Yellowstone National Park and found that nests within 1 km of campsites were less successful than those beyond this distance. Following this observation, 9 backcountry campsites near osprey nests were closed which resulted in an nesting success comparable to undisturbed nests. Likewise, Ream (1976) noted that both canoeists and common loons(*Gavia immer*) prefer to camp and nest

on islands in the Superior National Forest. She suggested that the mere presence of campers on islands may be a key factor in limiting loon reproduction. A factor which affected the reproductive success of prairie falcons (Falco mexicanus) in the Mojave Desert was the amount of time required to walk to the nest from the nearest road (Boyce 1988). This indicates that the degree of isolation from hikers can be important in nesting success of birds.

Boating: During any time of the year, boating may deprive animals of roosting or feeding habitat, whereas, in the breeding season it may cause reduced reproductive success or displace animals from breeding areas. The total number of boats and people may not be the best measure of recreational intensity because the presence of a single boat might be just as disturbing as that of many (Tuite et al. 1983, Knight and Knight 1984). Tuite et al. (1983) weighted various types of boating activity from most detrimental to least. This system considered motorboats as having the greatest disturbance potential because they involved both noise and movement while sailing and rowing were the least disturbing as they involved movement but no noise.

Titus and VanDruff (1981) illustrated how type of boating disturbance altered nesting success of common loons in Minnesota. A sport fishing season resulted in a sharp increase of motorboat activity on the larger lakes where loons nested. The main period of loon nest establishment occurred during the peak of recreational fishing. Interactions between loons and people were common because fishermen would troll or drift their boats along island and mainland shorelines (fishing usually occurred within 10 m of the shoreline). Slow trolling or extended use of a spot for fishing kept incubating birds off their nests resulting in nest desertion, predation, or embryo death. As sportfishing declined, there was an increase in canoe travel, which peaked in August. Canoe

travelers, however, usually did not have motors and used the area in different ways. Their objectives kept them away from lake shorelines and they moved quickly through an area from portage to portage. They rarely strayed off into the more remote parts of the lakes where the majority of the loon nests were found.

Vos et al. (1985) determined that experimental motorboat intrusions caused nesting great blue herons (Ardea herodias) to fly from their nests throughout the breeding season. Speedboats caused nest failures in ground-nesting ospreys where the incubating birds suddenly flushed from their nests dragging or breaking eggs (Ames and Mersereau 1964). Skagen (1980) reported a significant decrease in the proportion of bald eagles (Haliaeetus leucocephalus) feeding at a site when motorized boating occurred within 200 m of that area during the preceding 30 minutes. Motorized traffic apparently resulted in the abandonment of a nesting colony of anhingas (Anhinga anhinga) and great blue herons on a lake in Mississippi (Jackson 1983). Small boats with outboard engines caused wintering brant geese (Branta bernicla) to fly (Owens 1977). Recreational boaters on the Mississippi River disturbed staging flocks of canvasbacks (Aythya valisineria) on average 5.2 times a day which resulted in these birds flying up to 1 hour/day (Korschgen et al. 1985).

Nature viewing: There are no empirical studies which have examined the impacts of nature viewing on wildlife in wildlands. In a study of diverse water-related types of recreational activities in England, Tuite et al. (1984) found that birdwatching was the activity most associated with higher-than-expected numbers of waterbirds. Interestingly, this was explained by the fact that birdwatching, by its very definition, will occur in areas with high bird diversity.

Hunting/fishing/trapping: Hunting could potentially have important effects on behavior, population structure, and distributions of wildlife in wildlands (Cole and Knight 1990). The primary justification for hunting programs in wildlands is that wildlife populations demonstrate a compensatory response to predation, diseases and parasites, and competition. Excess individuals in a population will succumb to any one of these natural mortality factors so hunters can remove a segment of these "expendable" animals without harming the population. Batcheler (1968) demonstrated that compensatory responses were not shown by persecuted populations of red deer and chamois in New Zealand. He found that the normal responses to reduction in numbers (i.e., improved physical conditions, higher reproductive rates) were suppressed by the inability of the remaining individuals to use preferred components of the habitat. Following the cessation of hunting significant changes in sex ratios were observed with the adult sex ratio returning to 1:1 (Douglas 1971).

Murphy et al. (1990) examined whether hunting of dall sheep (Orvis dalli) in Alaska affected either the survival of young rams or lamb and yearling production as hypothesized by Geist (1971:296); survival of young rams and production of lambs and yearlings did not appear to be affected.

Hunting may alter the behavior of wildlife. Two years after intensive hunting of red deer and chamois had ceased, these populations ceased nocturnal feeding and recommenced diurnal feeding on open grassland slopes, the condition which existed prior to hunting began (Douglas 1971). Likewise, other investigators (King and Workman 1986, Jeppesen 1987a, 1987b, 1987c) have found that hunted populations of ungulates become more shy and wary, stay close to cover and feed in the open mainly at night.

Hunting affects the spatial and temporal patterns of bird populations. Hunters in Denmark caused birds to avoid preferred feeding sites and feed more during the night (Madsen 1988). Indeed, on nights when shooting had not occurred during the previous evening, there were six times more ducks present than compared to nights when there had been shooting the previous evening. Newton and Campbell (1973) noted a similar response in geese to hunting in Scotland; geese usually avoided feeding in fields where shooting had occurred for several days. Thornburg (1973) investigated the relationship between hunter activity and diving duck movements along the Mississippi River and determined that movements and distribution were determined by two factors: hunting activity and food availability. Altered spatial distribution patterns were associated with the opening of duck hunting season. Early morning and late evening flights consistently occurred before and after shooting hours.

Fishing is considered to be less disturbing to wildlife than either hunting or motorized boating (Tuite et al. 1983). Fishing, when not in a motorboat, is both silent and does not involve movement. Fishing from the shore has the greatest impact on waterfowl, at least when compared with other land-based activities such as bird watching, and picnicking (Newbold 1977, Bell and Austin 1985). Anglers remain stationary along a shoreline for long periods and intersperse these periods of relative inactivity with short periods of rapid movements. Angling on Llandegfeed Reservoir in South Wales was shown to displace several species of waterfowl from preferred feeding areas (Bell and Austin 1985). Angling was also shown to depress the feeding rates of waterfowl (Cramp and Simmons 1977, Cryer et al. 1987). Anglers influenced both the numbers and behavior of three avian scavengers in Washington (Knight et al. 1991). For each species, there were fewer present when anglers were present, and for bald eagles

and common ravens (Corvus corax), there were fewer feeding when anglers were present. Crows (Corvus spp.), however, were more likely to be found feeding when anglers were present; this was due to their ability to coexist spatially and temporally with humans (Knight et al. 1987).

As with hunting and fishing, trapping could cause alterations in both numbers and distribution of furbearers, however, there is little indication that such changes occur. Raccoons did not show statistically significant differences in habitat usage prior and during a trapping season (Glueck et al. 1988). During the first two weeks of the season, when trappers took 89% of the harvested animals, mean home range area was not different from the preseason mean value.

Rock climbing/mountaineering/spelunking: Cliffs and mountains are important topographic features in landscapes that tend to concentrate a diverse fauna (Maser et al. 1979). Cliffs may benefit wildlife directly by providing shelter, nesting and denning sites, and cover, or indirectly by influencing vegetation structure and diversity. Cliffs and mountains also may concentrate a variety of reptiles, birds, and mammals into a relatively small, specialized habitat, which, in turn, attract predators.

In recent years, the popularity of rock climbing and mountaineering has increased substantially, as evidenced by the proliferation of guidebooks of climbing areas (Vogel 1986, 1987). Rock climbing and mountaineering have the potential to disrupt wildlife populations because they overlap both spatially and temporally with critical periods of wildlife use of cliffs. Rock climbers choose routes that follow cracks and utilize ledges; features that are commonly used by breeding and roosting wildlife. Ledges and cracks often support what little vegetation is found on cliffs and mountains. This vegetation is removed by climbers as it hinders their climbing abilities, yet it can be important to

wildlife as perching, feeding, or nesting sites.

Temporal overlap also occurs because the most popular time to climb mountains and cliffs coincides with the peak of the breeding season for many wildlife species. For example, spring and summer is when most birds are nesting; this is also the ideal time for rock climbing as cliffs are free of snow and ice and the weather is favorable for climbing.

In a study which investigated the factors influencing nesting success of prairie falcons in the Mojave Desert, Boyce (1988) reported that the climbability of nesting cliffs influenced nesting success. Rock climbing was responsible for the abandonment of two peregrine falcon (Falco peregrinus) eries in Colorado (Enderson and Craig 1974).

Cave exploration has also increased in popularity and has been reported to be responsible for the decline of sensitive wildlife populations. Caves are used by many species of bats as roosting and maternity sites. Declines in gray bat (Myotis grisercens) numbers are attributable to disturbance by recreationists (Tuttle 1979, Rabinowitz and Tuttle 1980).

Bathing/swimming/beaches: The recreational use of beaches may displace wildlife populations as well as altering communities. Approximately 85% of Virginia beaches are "protected" under the ownership of conservation organizations, whereas, 75% of oceanfront in New Jersey allows unrestricted recreation (e.g., bathing). Over 80% of four beach-nesting seabirds (common tern [Sterna hirundo], least tern [Sterna antillarum], black skimmer [Rynchops niger], and herring gull [Larus argentatus]) in coastal Virginia nests on natural barrier island beaches while in New Jersey the vast majority have been displaced to dredge-composition islands and natural marsh islands (Erwin 1980). Along beaches in Nova Scotia, human disturbance (pedestrians and vehicles) was

implicated as a causative factor in the decline of piping plovers (<u>Charadrius</u> <u>melodus</u>)(Flemming et al. 1988) because increased disturbance resulted in lower chick survival.

Recreational development (campgrounds/cottages): Campgrounds, cottages, and other types of recreational development are often concentrated in riparian areas or other important wildlife habitats because of the presence of water, accessibility, fishing and nature-viewing opportunities, and aesthetic reasons. Accordingly, these developments may have inordinate impacts on wildlife in wildlands. In a comparative study of campgrounds and noncampground areas, Blakesley and Reese (1988) found that there were birds associated with each of the two areas that were generally not found in the other. Several of the species associated with campground were considered to be habitat generalists (e.g., American robin [<u>Turdus</u> <u>migratorius</u>], gray catbird [<u>Dumetella</u> <u>carolinensis</u>], yellow warbler [<u>Dendroica</u> <u>petechia</u>]), whereas species found in noncampground areas were considered to be more wary of humans (e.g., fox sparrow [<u>Passerella</u> <u>iliaca</u>])(Garton et al. 1977). Other than human disturbance, the main causative factor offered to explain these differences were the lower amount of understory vegetation and ground litter found in campgrounds.

The bird communities at six lakes in southern Ontario with different levels of cottage and recreational development were studied (Robertson and Flood 1980). Developed areas had significantly more birds and undeveloped sites, however, they also had lower species diversity than undeveloped areas. Species richness remained fairly constant in both areas whereas species evenness was significantly lower in the developed areas.

Campgrounds, resorts, and cottage developments along lakes in Alberta were negatively associated with numbers of breeding pairs of common loons (Vermeer

1973). Heimberger et al. (1983) found that hatching success in common loons declined as the number of nearby tourist cottages increased along the shores of northern lakes, presumably the result of increased levels of human activity and disturbance. Likewise, Lehtonen (1970) ascribed the decline of Arctic loons (Gavia arctica) in southwestern Finland to increasing numbers of summer cottages and boating activities.

Bald eagles prefer to locate their nests close to riparian areas, however, Fraser et al. (1985) found that eagle nests in Minnesota with shoreline homes were 80-1200 m from water while nests in areas without homes were only 10-400 m from water. This relationship was stronger for clusters of houses than for single homes. Clustered homes were inhabited throughout the year, whereas single homes were hunting cabins used primarily in the autumn.

Pets: Pets are being increasingly viewed as undesirable in wildlands. This is not only because they chase wildlife, but also because they kill it (McMurry and Sperry 1941, George 1974, Lowry and McArthur 1978). Grace (1976) noted that wolves (Canis lupus) on Ellesmere Island were chased by domestic dogs (Canis familiaris) and, in general, avoided them. MacArthur et al. (1982) noted that the greatest increase in heart rates of bighorn sheep were when they were approached by a human with a dog. Chamois in Austria showed more curiosity than fear in response to approaches by dogs (Hamr 1988). This was believed due to the long absence of wolves in the alpine habitat. Finally, Hamerstrom et al. (1965) noted that prairie chickens (Tympanuchus cupido) showed a stronger fear response to domestic dogs than to native predators such as red foxes (Vulpes vulpes). Of 41 visits by foxes to leking areas, only three caused all of the chickens to flush, whereas, of 25 visits by dogs, 13 caused total flushes.

Aircraft: Wildlife response to aircraft is influenced by many variables including aircraft size, color, proximity, flight profile, engine noise, and sonic booms (Smith et al. 1988). The two broad categories of aircraft, fixed and rotary-winged, have different disturbance potential. Rotary-winged aircraft and smaller fixed-winged aircraft fly slower and at lower altitudes. Accordingly, they may be more likely to disturb wildlife. The large, fixed-winged aircraft used by commercial and military organizations fly at greater altitudes and faster speeds. These type of aircraft should have little disturbance potential except during takeoff and landing, and when creating sonic booms.

Chamois in Austria did not respond to high-flying, large passenger aircraft, however, low-flying, light aircraft (helicopters, glider planes, hang-gliders) evoked strong responses, causing panic in groups of females with kids (Hamr 1988). The occurrence of these types of aircraft were infrequent in the area. Hamr suggested this strong reaction to aircraft was the result of traditional predation by eagles. Bighorn sheep showed no changes in their heart rates to rotary-winged or fixed-winged aircraft at distances beyond 400 m. Heart rates of sheep, however, increased 2-3 times when helicopters passed by directly overhead at heights of 90-250 m (MacArthur et al. 1982).

Dunnet (1977) found no evidence to suggest that aircraft (both fixed-wing and rotary-winged) flying at elevations of about 100 m above a mixed seabird colony (mainly kittiwakes [Rissa tridactyla], and guillemots [Uria aalge]) affected the abundance of birds. All six species at the colony appeared equally undisturbed. Kushlan (1979) found that fixed-winged and rotary-winged flights as low as 60 m over a mixed colony (mainly heron species) in Florida did not adversely affect the birds. Kushlan noted, however, that fixed-winged aircraft had been used for 20 years in southern Florida, without noticeable impact on bird

colonies and suggested that the study colony had habituated to this form of
disturbance.   Aircraft (type of aircraft unspecified) flights over a white
pelican (Pelecanus erythrorhynchos) colony in British Colombia during the
incubation period significantly reduced clutch size by frightening and stampeding
pelicans from their nests resulting in crushed eggs (Bunnell et al. 1981).
Aircraft flights later in the nesting period had no effect on clutch size.
Fixed-winged flights (heights unspecified) over bald eagles on nests in Minnesota
almost never caused adults to flush (Fraser et al. 1985). Any plane below 500
m and up to 1.5 km away would put flocks of wintering brant geese to flight
(Owens 1977).   Slow, noisy aircraft were especially harmful, while helicopters
caused widespread panic. Owens suggested that the strong response of geese to
aircraft, and their reluctance to habituate to planes, was partly due to the
visual resemblance of aircraft to large birds.

Vehicles/snowmobiles/motorcycles/ORVs/roads and highways: Vehicles, whether
on or off highways, appear to be one of the most detrimental types of
recreational activities impacting wildlife. As evidence of this, between 1973-74
and 1982-83 there was a 50% increase in vehicles per day using the main road
through Denali National Park in Alaska. This increased traffic volume correlated
with a 72% decrease in moose sightings per trip, and a 32% decrease in grizzly
bear (Ursus horribilis) sightings; sightings of dall sheep and caribou (Rangifer
arcticus) remained constant during this time interval (Singer and Beattie 1986).
Allowing unlimited vehicle access during fall of 1982 and 1983 had little effect
on the numbers of wildlife seen, however, more wildlife were put to flight,
flight distances increased, and more grizzlies were prevented from crossing the
road. Finally, moose (Alces alces) were found to be alert four times as often
when close to park roads than when over 1 km away.

Chamois in Austria were put to flight by vehicles at distances of 300-500 m, however, when in forests, chamois could be approached in a vehicle to within 30 m and often escaped only after a person stepped out of the vehicle (Hamr 1988). Mountain goats (Oreamnos americanus) were frequently prevented from crossing a highway in Glacier National Park, Montana, due to road traffic (Singer 1978). They were forced to change their initial approach to the highway as well as cross at different sites. They also shifted their diurnal patterns and more often attempted highway crossings at crepuscular times. During periods of peak recreational use in the Sheep River Wildlife Sanctuary, Alberta, bighorn sheep encountered 25-30 vehicles per hour. Behavioral reactions of sheep to vehicle passes were minimal; less than 1% (n=215) evoked withdrawal responses by sheep. Likewise, less than 9% of these encounters caused an increased heart rate (MacArthur et al. 1982).

Roads in black bear (Ursus americanus) habitat in western North Carolina increased bear mortality. Hunters drove slowly along roads with "strike dogs" searching for fresh bear scent. Bears that frequent roads, therefore, had a greater likelihood of being pursued and killed (Brody and Pelton 1989). Brody and Pelton (1989) found that in these areas, there was a negative relationship between human use of roads and bear use. Bears were more likely to cross roads of low traffic volume than roads with high traffic volume. Wolves within the Great Lake region of North America do not occur in areas with road (passable by 2-wheel-drive vehicles) densities > 0.61 km/km^2 (Thiel 1985, Jensen et al. 1986, Mech et al. 1988). It is not the roads themselves that prevent wolves from residing in these areas (other than the direct danger to wolves from vehicle impact [De Vos 1949]) but rather that roads allow accessibility to humans who either deliberately, accidentally, or incidentally kill wolves by shooting,

snaring, or trapping (Mech et al. 1988).

Yarmoloy et al. (1988) disturbed radio-collared mule deer (Odocoileus hemionus) with an all-terrain-vehicle and noted that harassed deer, but not control animals, altered feeding and spatial-use patterns. Additionally, the disturbed deer, unlike the controls, experienced lower reproduction the following year.

A number of biologists have examined the effects of snowmobiles on white-tailed deer (Odocoileus virginianus). These studies have taken place in harsh winter environments where abiotic factors (e.g., cold, snowfall) might be expected to play an important role in wildlife survival. Dorrance et al. (1975) had two study areas in Minnesota: one where snowmobile use averaged from 10-195 per day while the other prohibited snowmobile use. The effects of snowmobiles on deer in the area of heavy use resulted in the displacement of deer from areas immediately adjacent to snowmobile trails. The effects of snowmobile traffic on deer in the other site, however, were pronounced. Here snowmobiles resulted in increased home range size, increased movement and displacement of deer from areas along trails. Dorrance et al. speculated that during severe winters on poor ranges, the displacement of deer from even small segments of their home ranges could alter the energy balance of deer and reduce survival.

Eckstein et al. (1979) studied the effects of snowmobilers on deer in two Wisconsin deer yards, neither of which had been previously used by snowmobilers. They found no differences in home-range size and habitat use in areas with and without experimentally-introduced snowmobile activity.   Snowmobiling did, however, cause some deer to leave the immediate vicinity of snowmobile trails.

Richens and Lavigne (1978) suggested deer management could be enhanced by use of snowmobiles. This was because white-tailed deer used snowmobile trails

as travel routes to feeding and bedding sites. Because the energy expended by deer walking in snow increased with increasing sinking depth (Mattfeld 1973), Richens and Lavigne suggested that the packed surface of snowmobile trails reduced the energy expenditure of travelling deer.

Off-road vehicle use in the Mojave Desert of California was negatively associated with nesting success of prairie falcons (Boyce 1988). Nesting great blue herons abandoned (67% of 12 trials) their nests temporally to experimental trials in which a motorcyclist passed by the colony (Vos et al. 1985). Roads in Denmark with traffic volume of 20-50 cars per day had a depressing effect on pink-footed goose (Anser brachyrhynchus) utilization of fields up to 500 m from the road (Madsen 1985). Although this study dealt with motorized traffic on primary highways, instead of off-road vehicles, it supports the negative effects of vehicles. A similar study in Germany found that wintering bean (Anser fabalis) and white-fronted geese (Anser spp.) maintained distances when feeding of from 500-800 m from highways (Mooij 1982).

ORV use in the Mojave Desert, California, affected species diversity of the lizard community. Callisaurus draconoides occurred only in a moderately disturbed area, C. wislizenii was found only in the undisturbed plot as where Uta stansburiana and Cnemidophorus tigris (Busack and Bury 1974). Only a few individuals of one species were found in the heavy ORV use area.

Researchers: It is difficult to imagine a field of study which has received more work than the impacts of researchers themselves on the wildlife they study. Perhaps this is because scientists are generally quick to realize the opportunities for experimental studies and their own visitation rate and duration can be experimently manipulated. The activities of investigators may impact wildlife in a number of different ways: they may alter animal behavior, alter

animal reproductive biology, alter animal foraging ecology, alter population size and structure, and alter community structure.

Red-winged blackbirds (Agelaius phoeniceus), American goldfinches (Carduelis tristis), and American robins altered their nest-defense behavior because of researchers (Knight and Temple 1986a, Knight and Temple 1986b, Knight and Temple 1986c). Nest-defense intensity was significantly more aggressive by adults whose nests had been visited repeatedly by researchers than at nests not visited. Adult red-winged blackbirds learned to distinguish between people who visited their nests often and people who had not previously visited the marsh; the blackbirds responded much more aggressively to the familiar people.

Predators may learn to follow human scent trails to nest sites (Earl 1950, Hammond and Forward 1956, Willis 1973, Mayfield 1975, Gottfried and Thompson 1978). Avian predators have learned to locate the nests of other species by the markings researchers have used to relocate nests (Picozzi 1975, Reynolds 1985). Finally, avian predators apparently learn to forage in the vicinity of investigators who are visiting bird nests, taking advantage of the flushed adults and the exposed nests (MacInnes and Misra 1972, Strang 1980).

Wildlife may alter subsequent nest placement based on prior experience with humans (Marzluff 1988). Some birds locate nests higher above the ground if they have been disturbed by human intruders in the past (Stoner 1937, Hickey 1942, Preston and Norris 1947, Ratcliffe 1962), although the evidence has been circumstantial. Black-billed magpies (Pica pica), in response to investigators climbing to their nests, altered the placement of their nests in subsequent years, attempting to make them more inaccessible to human beings (Knight and Fitzner 1985). There were no changes in nest placement at nests not climbed.

Lennington (1979) reviewed data from 16 studies of red-winged blackbirds that reported reproductive data from two or more consecutive years. Eleven of these studies were in marsh habitats while the remainder occurred in upland sites. The proportion of successful nests was lower in the second year of the study than in the first for 10 of the 11 marsh studies, with an average decline in the proportion of successful nests of 22.9% (range: 6-50%). Four of the marshes were studied for three or more consecutive years and the increase from the second to third year was not as large as that between the first and second year. The impact of human activity on nest predation was not as clear for upland sites as in marsh habitats. Lennington (1979) suggested this might be due to lower nesting densities in upland habitats than in marsh areas.

Bart (1977) analyzed data from the North American Nest Record Card Program at the Laboratory of Ornithology at Cornell University and found that for four of five species there was a clear impact of researcher nest visits on nest survivorship. Later he reported that his results could also be explained by reporting bias (Bart and Robson 1982). Others have concluded, however, that investigator disturbance at nests decreases nest or nestling survivorship, provokes nest abandonment or discourages renesting (Evans and Wolfe 1967, MacInnes and Misra 1972, Willis 1973, Gillett et al. 1975, Robert and Ralph 1975, Ellison and Cleary 1978, Tremblay and Ellison 1979, Bunnell et al. 1981, Westmoreland and Best 1985, Salathe 1987, Piatt et al. 1990).

Gottfried and Thompson (1978) found that daily visits to artificial nests did not affect whether they were discovered by predators. Likewise, other investigators failed to find that visiting nests led to increased nest failure or decreased nestling survivorship (Evans and Wolfe 1967, Gates and Hale 1975, Grier 1969, Morris and Hunter 1976, Livezey 1980, Poole 1981, Gotmark and Ahlund

1984, Galbraith 1987, Gotmark et al. 1990, MacIvor et al. 1990, Sedinger 1990).

There is some indication that human activity may actually increase reproductive success of wildlife. High and predictable levels of human activity may exclude predators from gaining access to bird nests. Blackbirds (Turdus merula) nesting in urban England had higher nesting success closer to human activity than birds which nested further away (Osborne and Osborne 1980). Likewise, morning doves (Zenaida macroura) had higher nesting success in orchards with high levels of human activity than doves breeding in orchards with little or no human activity (Knight et al. 1984).

Mortality rates of wildlife can be elevated through association with humans. Nestlings of Cooper's hawks (Accipiter cooperii) that had some type of intensive study (e.g., handling by humans, study from blinds) by researchers suffered a significantly higher mortality rate after fledging than nestlings from nests which were not exposed to frequent human contact (Snyder and Snyder 1974).

Other: There are other types of human activities that may perturb wildlife in wildlands, but that do not conveniently fall within the above categories. Among these are military activities. Military reservations comprise a substantial part of the United States and contain a significant amount of natural or semi-natural lands. Military training activity displaces animals from their accustomed home ranges. Red-tailed hawks (Buteo jamaicensis), Swainson's hawks (Buteo swainsoni), ferruginous hawks (Buteo regalis), and golden eagles (Aquila chrysaetos) all shifted the center of their home range and activity areas and increased the size of the area they used during military training exercises (Andersen et al. 1986, Andersen et al. 1990).

ORIGIN OF RESPONSES OF WILDLIFE TO RECREATIONISTS

Learned

Because of the nature of interactions between recreationists and wildlife, learning should be expected to be important in shaping wildlife responses to an array of activities. As an example of how learning may influence wildlife behavior and create management dilemmas, consider that consumptive and nonconsumptive uses of ungulates, such as bighorn sheep, are viewed by some as being incompatible (Geist 1975). This is because hunting results in wildlife avoiding humans while nature viewing requires wildlife to habituate to people. Both of these responses, habituation and avoidance, are the result of learning (Eibl-Eibesfeldt 1970). In areas open to hunting, black bears avoid roads (Reiffenberger 1974, Hamilton 1978, Brown 1980, Villarrubia 1982, Brody and Pelton 1989), whereas, in areas where bears are protected from hunting, bears are attracted to roads because of human food wastes. Geist (1978) has pointed out that if people are to mix in wildlands with wildlife, then it is important that wildlife habituate to humans. If wildlife, however, associate either rewards or punishments with people, then the desired effect will be detrimental. In these cases, wildlife will either seek out humans or avoid them. The three types of learned responses wildlife may show to recreationists are habituation, attraction, and avoidance.

Habituation: The simplest form of learning is habituation which is defined as a waning of a response to a repeated stimulus which is not associated with either a positive or negative reward (Eibl-Eibesfeldt 1970). A positive reward would result in attraction, whereas, a negative response would result in avoidance. Although there is abundant anecdotal evidence that animals do habituate to human beings, very little experimental data exists. Knight and

Knight (1984) attempted to verify whether bald eagles habituated to people (Stalmaster and Newman 1978, Russell 1980, Skagen 1980). They studied differences in flushing responses of bald eagles on two adjacent rivers, one with a large amount of recreational boating and the other with none. Eagles were much less inclined to flush from boaters on the heavily travelled river suggesting that eagles had habituated to boaters. However, because Owen (1972) and Skagen (1980) had suggested that food levels influenced wintering white-fronted geese and bald eagle responses, respectively, to human activities, Knight and Knight compared the available food (i.e., spawned salmon carcasses) between the two rivers. They found that the river with heavy recreational traffic also had nine times less food than the undisturbed river. Accordingly, they were unable to determine whether eagles habituated to boating activities or responded to decreased food abundance by an increased reluctance to fly.

To examine whether eagles habituated to human activities would require: (1) areas that differed in levels of human activities but that were similar in other biotic and abiotic conditions; (2) eagles in residence long enough to become habituated; and (3) eagles that were not being either actively punished or rewarded (Knight and Knight 1984). In the face of active persecution (e.g., shooting), it would be maladaptive to habituate.

Knight et al. (1987) took advantage of a natural experiment to see whether American crows (Corvus brachyrhynchos) habituated to humans in an area of high human density and low persecution (i.e., cities). They hypothesized that in the absence of persecution, but in the presence of high human activity, crows would have to habituate in order to complete their daily activities. They compared the responses of crows to humans on the ground both in a city and in a rural area, where crows were actively persecuted. Crows in the city ignored humans on the

ground indicating they had indeed habituated to nonthreatening activities.

Ungulates may become habituated to predicable events such as highway traffic, which they learn is not dangerous. Likewise, they may become accustomed to activities like jogging and hiking on forest roads and trails. Nonetheless, stray dogs and humans away from roads and trails are unpredictable and ungulates will not habituate to these activities (Geist 1978, Geist et al. 1985). MacArthur et al. (1979) felt that bighorn sheep had habituated to humans due to the frequent exposure of sheep to humans coupled with the absence of hunting. Likewise, a nonhunted population of bighorn sheep in California which was frequently exposed to hikers became conditioned to human activity (Hicks and Elder 1979). Mule deer in British Columbia habituated to all-terrain vehicles travelling along a predictable route, whereas, deer pursued by vehicles responded with noticeable behavioral and reproductive changes (Yarmoloy et al. 1988). Eckstein et al. (1979) reported that snowmobile activity had little effect on the overall winter movements of white-tailed deer, and suggested this was due to deer becoming accustomed to the noise of machinery and power-saws from winter logging operations. Richens and Lavigne (1978) also reported that deer became conditioned to snowmobile activity. Chamois appeared to habituate to humans as long as the intruders' activities remained spatially and temporally predictable (Hamr 1988). Singer and Beattie (1986) suggested that caribou, grizzly bears, and moose had partially habituated to human activities over time.

Birds also habituate to stimuli that are predictable and nonthreatening. Brent geese quickly became habituated to most sounds, however, unexpected sounds (e.g., gun shots) quickly put geese to flight (Owens 1977). Vos et al. (1985) reported that great blue herons habituated to repeated, nonthreatening activities such as fishermen boating past a heronry. Unexpected disturbances, however, put

the herons to flight. Unlike herons nesting in an area of high human activity, nesting white pelicans at a remote lake in British Columbia did not habituate to human activities and showed strong flight responses (Bunnell et al. 1981). In areas of high levels of human activity, nesting ospreys habituate to many of these activities, however, in more remote sites where human presence may be abrupt and sporadic, ospreys apparently do not habituate (Swenson 1979, Poole 1981).

Attraction: Attraction is defined as the strengthening of an animal's behavior because of rewards or reinforcement. Examples of sensitization are evident in most wildlands where recreationists may occur. Whether it be a chipmunk, bird, or gray jay (Perisoreus canadensis), wilderness travelers are accustomed to encountering wildlife which approach them for some form of food reward. An extreme example of this is where caribou follow the sound of chain saws of logging operations to order to feed on the lichens of downed trees (Klein 1971, Bergerud 1974). Birds which are attracted to food sources created by humans were most abundant near campgrounds, whereas, birds which did not utilize human food were not (Blakesley and Reese 1988). Ravens nested close to human residences in Virginia because of human-generated food (Hooper 1977). Ravens that did nest close to humans had higher reproductive success than those nesting elsewhere.

Attraction by wildlife to humans is usually harmful to wildlife. In the extreme case, where attraction brings into contact humans and potentially-dangerous animals, it results in the "problem" animals being killed. The occurrence of black bear incidents at backcountry sites was associated with high numbers of visitor-nights (Singer and Bratton 1980). In other cases, it may alter some important aspect of the animal's behavior, such as foraging, which,

in the absence of the food reward, could alter the animal's survival. Wolves frequented a weather station on Ellesmere Island because of human food wastes left at a garbage dump (Grace 1976). Grace speculated that if a widespread dump-foraging habit erose among wolves it might impair their health as well as decrease their effectiveness as natural predators.

Perhaps the best documented example of a species which showed attraction behavior to human beings is the grizzly bear in Yellowstone National Park. Up until the early 1970s a portion of the park's grizzly bear population subsisted, to varying degrees, on human food wastes at garbage dumps within the park. Following the sudden closures of the dumps by the National Park Service there were expansions in the size of bear home ranges, and decreases in body size, reproductive rate, and average litter size (Despain. et al. 1986). The change in nutrition from human food wastes to natural foods may explain a number of these life-history differences. In addition, once the dumps closed, bears had to relearn skills required to obtain live prey and carrion. As Despain et al. (1986) explained 'In a garbage dump situation, the most successful feeder might be the bear that can best defend a pile of potatoes from other bears; in a hunting situation, the most successful feeder might be the bear that can best chase and catch elk (Cervus canadensis).'

At the extreme view of this argument, there is the possibility that attraction behavior in a keystone species could even alter an ecosystem. Tomback and Taylor (1986) studied Clark's nutcrackers (Nucifraga columbiana) at scenic turnouts in Rocky Mountain National Park where tourists feed these birds. Nutcrackers are an important dispersal agent for limber pine (Pinus flexilis), a common species in the subalpine ecosystems of the Front Range of Colorado. They speculated that if tourist activities discouraged normal nutcracker seed

harvesting and storing activities, a decline in afforestation rates was possible.

The fact that attraction behavior has created management problems for natural resource agencies is well appreciated. Wildlife which are potentially harmful to human beings (e.g., grizzly bear), and that seek out humans for food, can create dangerous situations for recreationists (Herrero 1970). For example, of 107 personal injuries of humans by black bears in Great Smokey Mountains National Park, 35 occurred while people were either feeding or petting bears (Singer and Bratton 1980). These, and situations with less grave consequences to humans, have encouraged natural resource agencies to attempt to alter recreationists' behavior so they do not reward wildlife for close approaches.

Avoidance: Whereas animals might be expected to habituate to a novel stimulus, they should learn to avoid a stimulus associated with pain or punishment. Perhaps the best example of this is the impact of active persecution on wildlife. Hunting has resulted in pronounced behavioral shifts in wildlife; including the alterations in foraging ecology and habitat use. Roe deer subjected to hunting in Denmark were more wary and secretive than deer in populations were hunting was prohibited (Jeppesen 1987a, Jeppesen 1987b). Likewise, Batcheler (1968) noted that hunting red deer and chamois in New Zealand resulted in animals becoming wary, shifting their foraging patterns to feed at night, and shifting their distribution to dense timber. As an indication that this was a learned response, two years after intensive hunting had ceased, both species had recommenced diurnal feeding on open grasslands (Douglas 1971).

Desert bighorns which have been hunted fled at greater distances and showed wary behavior for longer periods of time following disturbances (King and Workman 1986). Hamr (1988) noted that chamois increased their sensitivity to

disturbances with an increased frequency of harassments. Grizzly bears in Glacier National Park moved away immediately from people only 5% of the time, whereas, in an adjacent area outside the park, where they were persecuted, bears always moved away immediately, and on most occasions, they fled >1 km or further (McLellan and Shackleton 1989).

The hypothesis that in areas of high persecution wildlife should show avoidance behavior to humans was examined for ravens and crows (Knight 1984, Knight et al. 1987). Ravens nesting in an area of high persecution were more timid and showed stronger avoidance behavior and lower nest defense than ravens in areas of low persecution. Likewise, crows that were actively persecuted showed less aggressive nest-defense behavior than crows which were not persecuted.

Number and outcome of interactions with humans: Even a cursory review of wildlife responses to human activities reveals an enormous amount of inter- and intra-specific variation. For example, Suter and Joness (1981) asked 74 raptor biologists to list distances at which three raptor species responded to different stimuli. Distances reported ranged over a factor of 45. A population of peregrine falcons in New Mexico showed differences by a factor of 22 in the distances at which they responded to stimuli (Johnson 1988). Flight distances among bald eagles differ geographically as well as seasonally (Knight and Knight 1984, Fraser et al. 1985). Moose in Denali National Park were more alert to vehicle traffic than were caribou (Singer and Beattie 1986). In The Netherlands, recreation activity negatively influenced eight species of passerines, whereas, five were not affected (van der Zande et al. 1984).

This wide range in intra- and inter-specific variation must certainly have both innate and learned components. Species differ in their learning abilities

as well as differ in their innate responses to similar stimuli. The learned component of this variability has been attributed to the number and outcome of interactions between individuals and stimuli over the individual's lifetime (Newton 1979, Poole 1981, Buitron 1983, Fraser 1984, Knight and Temple 1986c, Knight and Knight Skagen 1988). King and Workman (1986) found that desert bighorn sheep increased their avoidance responses to human beings with an increasing number of negative encounters. Red-winged blackbirds, American robins, and American goldfinches whose nests were repeatedly visited by researchers became significantly more aggressive over time (Knight and Temple 1986b, 1986c). Parent birds at nests visited only once, but at equivalent time periods during the nesting season, did not show elevated levels of aggressiveness. Parents at nests visited repeatedly were rewarded by their aggressive nest defense in that the researchers always left their nests intact. Nesting ferruginous hawks flushed at greater distances to humans in the second year of a study investigating the effects of disturbance (White and Thurow 1985). Bald eagles flew at increasing distances to observers repeatedly approaching their nests (Fraser et al. 1985). Owens (1977) and Madsen (1988) found that when Brant geese were frequently disturbed, they became more easily disturbed on subsequent occasions. Pink-footed geese also showed increased wariness with an increase in harassment (i.e., hunting)(Madsen 1985).

These findings, and the studies listed under the three types of learning described earlier, all support the concept that learning is the result of the number and outcome of interactions between an individual and its environment over the individual's lifetime. Additional variables must also influence an animal's responses, for example, the individuals it is associated with, its motivational state, the degree and intensity of disturbance, etc.

Genetic

In addition to learning, animals have an innate or genetic component affecting their responses to stimuli. Unlike learning, the innate responses of a species will be performed in a uniform and stereotyped fashion. It should be stressed that an animal's behavior is very much the product of both the innate and learned components. Innate behaviors are genetically determined, whereas, learned behaviors are environmentally mediated. Hailman (1967) developed this idea in his concept of "learning of an instinct." Animals are genetically predisposed to certain behaviors which are in turn influenced by environmental learning. For example, bighorn sheep and mountain goats withdraw to cliffs when they heard sudden loud noises, apparently an innate response to avalanches and rockfalls (Geist 1971, Geist 1978). This genetically-determined behavior can be reinforced through learning by the discharge of firearms in a hunted population. Hamr (1988) believed that the alarm response shown by chamois to airplanes was due to an innate fear the species has to golden eagles.

Newton (1979) hypothesized that intraspecific differences in nest-defense behavior of Falconiformes were due to past levels of human persecution. If shooting disproportionately eliminated aggressive birds then nest-defense aggressiveness would vary with the history of persecution in an area. Newton implied that natural selection was the mechanism that modified a species' behavior. Although there have been laboratory experiments on the innate responses of animals to stimuli, there has been little work on this topic in wild populations. One attempt to address this question was by Knight et al. (1989) who compared nest-defense behavior in seven widely separated populations of red-tailed hawks in North America and that differed in the number of years since European settlement (range: 75-215 years). Length of European settlement was

assumed to correlate positively with the duration of persecution. Pre-European
persecution by native North Americans was assumed to be similar among areas and
was limited until the acquisition of firearms from Europeans. Knight et al. found
a close fit between the number of years since European settlement and the call
and dive-rates of hawks. Call rates were highest in the most recently settled
areas.

FACTORS THAT INFLUENCE THE NATURE AND MAGNITUDE OF WILDLIFE RESPONSES

Characteristics of the disturbance

Timing: The temporal pattern of disturbance can affect its impact on
wildlife. Traditionally, disturbance is considered to have the most negative
effect on wildlife during the breeding season. People hear from childhood that
disturbing a bird nest or young animal will result in parental abandonment.
Alternatively, the public has not appreciated that disturbing wildlife outside
of the breeding season may have equally severe effects.   There is a stark
contrast, however, between disturbance at these two times in an animal's annual
cycle.   Disturbance during the breeding season may affect that individual's
productivity; disturbance outside of the breeding season may affect the
individual's ability to forage and, therefore, its survival.   Disturbance at
either time of the year can affect an animal's inclusive fitness.

Breeding season - Disturbance during the breeding season can have
detrimental effects on the reproductive biology of wildlife. The most common
response to severe disturbance is nest or young abandonment which can lead to
total reproductive failure.   Because disturbance can cause adult birds and
mammals to leave their nests or den sites, human activity can also alter parental
attentiveness increasing the risks of the young being preyed upon, disrupting
feeding patterns, or exposing the young to severe environmental conditions.

White and Thurow (1985) reported 33% (eight of 24 nests) of disturbed ferruginous hawk nests were deserted whereas no undisturbed nests (n = 38) were abandoned (C. White, pers. commun.). Only 52% of the territories containing disturbed nests were occupied the year following disturbance, whereas, 93% of the territories containing control nests were reoccupied. Additionally, disturbed nests that were not deserted fledged significantly fewer young than undisturbed nests.

Swenson (1979) reported that nesting ospreys in Yellowstone National Park had reduced nesting success in areas where recreationists were common. Other researchers have attributed lowered reproduction in nesting ospreys to human disturbance (Dunstan 1968, Reese 1977, Van Daele and Van Daele 1982), although Ames and Mersereau (1964), McCarter (1972), French and Koplin (1977), and Poole (1981) found no relationship between disturbance and reproductive success.

At first these discrepancies in nesting success among ospreys appear paradoxical, however, there are several reasons which could account for the differences. For example, Poole (1981) reported no disturbance-related effects on osprey nesting success while Swenson (1979) did. Swenson reported that disturbance activity was high during the middle of the incubation period whereas Poole visited nests mainly after the eggs had hatched. Timing within the nesting cycle, therefore, may explain the discrepancies between these two studies. Other studies corroborate this suggestion (Tremblay and Ellison 1979, Bunnell et al. 1981).

Disturbance during the nesting season may cause reproductive failure in ways other than nest abandonment. If parents are disturbed from their nests, and are reluctant to return, then predators may visit the nest and consume eggs or young. Choate (1967) studied common eiders (Somateria mollissima) nesting in Maine and

noted that after humans left the nesting area, gulls returned much sooner than the eiders and preyed on eggs and young. Gull predation was over 200 times higher on creches of eider ducklings disturbed by boats than for undisturbed creches (Ahlund and Gotmark 1989).

Verbeek (1982) estimated that 22% of all eggs in first clutches of double-crested cormorants (Phalacrocorax auritus) were consumed by northwestern crows (Corvus caurinus). When bald eagles were present, more cormorant eggs were lost to crows than on days when eagles were absent. This was because flying eagles caused cormorants to leave their nests. Eagles were more likely to be seen flying on weekends than on weekdays, because of the increased levels of recreational boaters on weekends.

Little empirical information exists on the responses of mammals to disturbance during the breeding season.

Nonbreeding season - Outside of the breeding season animals are not tied to a nest or den site, nor are young as dependent upon their parents. Wildlife, however, still respond to disturbance thereby potentially minimizing energy acquisition (i.e., foraging) or increasing energy expenditure (i.e., fleeing)(Owens 1977).

A body of literature has accumulated on various aspects of recreational disturbance as it pertains to the energetics of wintering waterfowl. The central question has been whether or not waterfowl can compensate for the lost feeding opportunities due to disturbance. This is particularly important for those species that feed primarily on vegetation. The low digestive efficiency and caloric content of many plant food items may require certain species to forage for much of their available time (Owens 1977).

That disturbance causes waterfowl to redistribute has been shown (Thornberg 1973, Bell and Austin 1985, Cryer et al. 1987; but see Tuite et al. 1984). Without information on the nutritional and physiological effects of such disturbance, however, it is not possible to assess the long-term effects on waterfowl populations. It has been suggested, however, that departures from normal behavior are potentially adverse, and wintering waterfowl should be managed so as to minimize disturbance (Bell and Austin 1985, Belanger and Bedard 1989).

Processes influencing energy intake during winter have a much greater impact on energy balance of ungulates than processes affecting energy expenditure (Hobbs 1989). This suggests that disturbance which disrupts feeding wildlife should be of greater concern than disturbance which simply causes wildlife to flee. Mammals show less of a response to humans during winter than at during other seasons. Hamr (1988) reported that chamois were least sensitive to recreationists during winter when snow was deep, forage inaccessible, and energy conservation decisive to survival.

Location: The location of disturbance in relation to the location of wildlife can influence the response shown by an animal. Hikers approaching bighorn sheep from above were more likely to elicit a reaction than hikers approaching from below (Hicks and Elder 1979). Nesting peregrine falcons in the New York City region were not disturbed by recreationists at the base of their nesting cliffs, however, any approach by humans from above was immediately alarming (Herbert and Herbert 1965). Bald eagles on the ground were much more likely to fly, and flew at greater distances than eagles perched in trees (Knight and Knight 1984).

Frequency and magnitude: It is intuitively appealing to believe that if disturbance negatively affects wildlife, then the overall impact of disturbance on wildlife will depend on the frequency and magnitude at which disturbance occurs. Van der Zande et al. (1984) developed the concept of 'LD$_{50}$ recreation intensity' as an indicator of the level of recreation frequency above which a certain species will probably disappear from an area. The LD$_{50}$ for any species would be the recreation intensity which causes a 50% reduction of a wildlife population. They took this theoretical concept and modified it to reflect the number of recreationists/ha/day. Bird densities in The Netherlands decreased within recreation intensity values of 7.8 and 37.0 visitors ha^{-1} (van der Zande and Vos 1984).

Another indicator of recreation intensity was calculated by simply combining the totals of stationary and moving recreationists (van der Zande and Vos 1984). These RI (recreation intensity) values showed negative relationships with bird abundance.

A number of studies have compared reproductive success of birds whose nests are visited repeatedly versus visited infrequently. In each case the areas visited the most often suffered the lowest reproductive success (Choate 1967, Evans and Wolfe 1967, Robert and Ralph 1975, Tremblay and Ellison 1979, Bunnell et al. 1981).

High levels of white-tailed deer movement were associated with human activity levels of >0.45 hours/ha (Root et al. 1988). It was suggested that a frequency of human disturbance more than once per 20 years would cause a decline in a nesting population of white pelicans in British Columbia (Bunnell et al. 1981). An undisturbed population would slowly increase about 1% per year. Intensity of disturbance had a very clear effect on waterbird distribution in

South Wales (Tuite et al. 1983). Four species virtually abandoned preferred areas at levels of recreation which exceeded 75 boat/people hours (an average of 8-10 boats on a lake at any one time). Belanger and Bedard (1989) studied disturbance effects on staging greater snow geese (Chen caerulescens) during fall and spring in Quebec. They found rates of disturbance during the fall that averaged from 1.02/hr to 1.46/hr, mean time in flight of disturbed flocks averaged from 56 to 76 seconds, and mean time to resume feeding after being disturbed averaged from 122 to 726 seconds. Additionally, the level of disturbance that occurred on a given day influenced the number of geese using that area the following day. When disturbance exceeded 2.0/hr, it resulted in a 50% drop in the mean number of geese present the next day. They concluded that a reduction in feeding time because of disturbances could affect the distribution and the length of the staging period of greater snow geese along the Saint Lawrence estuary.

In additional work Belanger and Bedard (1990) found that daylight foraging time decreased by 4 to 51% depending on disturbance levels. A disturbance rate of 0.5/hour approximately doubled the flight time, while a maximum rate of 2.5/hour was estimated to cause a 5-fold increase in flight movements compared to undisturbed geese. Computed time needed to resume feeding was 5 times greater at a daily disturbance rate of 2.5/hour than at 0.5/hour. They concluded that there were would have to be a 32% increase in nighttime feeding to compensate for daytime disturbances that caused geese to flush and not return to feed. Pink-footed geese avoided using fields that were adjacent to roads with 20-50 cars/day; even highways with 10 cars/day had a depressing effect on field utilization (Madsen 1985).

Stalmaster (1983) prepared an energetics simulation model which quantified the effects of recreationists on wintering bald eagles in the Pacific Northwest. His model predicted that land- and water-based disturbances that resulted in avoidance flights cost eagles 0.0359 kcal and 0.359 kcal, respectively. For example, if 30 land and water activities occurred daily at a winter feeding site for 30 days while 300 eagles were present, 106,623 kcal would be expended in human-disturbance related avoidance flights thus reducing the area's carrying capacity by 217 eagle days (Stalmaster 1983).

Two aspects of disturbance magnitude which may affect wildlife response are speed and noise. There is a great degree of variability in wildlife response to noise. Certainly the context in which the noise is presented influences an animal's response. Wintering bald eagles disregarded most noises when they were visually shielded from the disturbing activity (Stalmaster and Newman 1978). Likewise, mountain goats disregarded the sounds of passing trains and visitors that they could not see (Singer 1978). There were no changes in heart rates of bighorn sheep to the sounds of automobile horns nor to commercial jet aircraft (MacArthur et al. 1979). Slow, noisy aircraft disturbed feeding Brent geese (Owens 1977). Slow, noisy motorboats disturbed nesting great blue herons whereas fast motorboats did not (Vos et al. 1985). Snowmobiles at high speeds frightened white-tailed deer more easily than at low speeds (<16 km/h), but stopping to view deer invariable resulted in fleer fleeing (Richens and Lavigne 1978). Burger (1981) found that human activities that involved rapid movement or close proximity to roosting water birds caused them to flush, whereas slow-moving human activities usually did not.

Predictability: The level of predictability associated with human activity at an area is extremely important in the response of wildlife to that activity. When disturbance is nonthreatening and frequent enough so as not to 'surprise' animals, it causes little response.   Both nesting bald eagles and ospreys were unaffected by humans in areas of frequent, nonthreatening human activity (Grier 1969, Poole 1981). Disturbance can also be predictable and threatening (e.g., active persecution) which would result in quite a different type of response from wildlife. Owen (1972) suggested that the level of wariness of a flock of geese feeding in a particular area may depend on the tradition of disturbance in the area. Geese and waterfowl are more likely to return and feed at areas where they feel safe (Newton and Campbell 1973). Whether hunting had occurred on a marsh the previous evening influenced whether ducks revisited that marsh (Madsen 1988). Knight and Knight (1986) documented decreased feeding efficiency of wintering bald eagles in areas of with a history of human presence when compared with areas devoid of humans. Bald eagles are actively persecuted (i.e., shot) in this area so the high level of human activity was no doubt viewed in a threatening context.

Number and composition of wildlife or humans: The number and composition of both recreationists and wildlife may influence the response of wildlife to disturbance. For example, group size of animals influences their responses to potential danger (Rubenstein 1978, Morse 1980, Pulliam and Caraco 1984). Animals feeding in groups respond to approaching threats at greater distances and are less vulnerable to attack than solitary individuals. In addition, individuals in flocks and herds can spend less time looking for threatening intruders and more time feeding without reducing their level of safety. The time devoted to vigilance by feeding individuals decreases as flock or herd size increases.

One might argue that larger flocks would result in individuals feeling more secure and allowing a closer approach, because of the 'selfish herd' effect (Hamilton 1971). Birds, however, show a positive correlation between flight distance to human intruders and flock size (Owens 1977, Batten 1977, Greig-Smith 1981, Madsen 1985). It is suspected that these variations in flight distances are due to differences in tolerance among flock members. There is an increased likelihood that larger flocks will contain individuals who are more sensitized to humans and will flush at a greater distance thereby causing other flock members to also flush. Group size did not, however, affect whether white-tailed deer fled or not to snowmobiles (Richens and Lavigne 1978). Likewise, group size did not influence flight distances of wintering bald eagles (Knight and Knight 1984).

Age and sex may also influence responses of wildlife to human beings. Cow/calf groups of caribou were more likely to flush than mixed groups which in turn were more likely to flush than cow groups. Bulls were the least likely to flush (Singer and Beattie 1986). Male chamois were more tolerant of disturbances than females, particularly during the periods of parturition and weaning (Hamr 1988). In addition, females with kids escaped sooner and withdrew further than yearling females or females without kids. Stalmaster and Newman (1978) observed that adult bald eagles flushed at greater distances than immatures and attributed this difference to experience; older birds had learned that humans were to be avoided. Subsequent studies, however, have been unable to identify an age effect in terms of flushing to human activity (Russell 1980, Knight and Knight 1984).

MANAGEMENT OPTIONS

Presently, two general approaches are used to minimize the effects of recreational disturbance on wildlife populations. One is to deny human access

to sensitive areas. This approach is generally only used in extreme cases where critically endangered or sensitive species occur. Often species which fall in this category are area-sensitive, that is, they have large home-range requirements. Excluding people from sizeable areas is difficult to enforce and often unpopular with recreationists.

The second approach is to devise management schemes that allow recreationists and wildlife to coexist. This is the most realistic approach in that it insures wildlife is still accessible to people, one of the primary reasons why recreationists visit wildlands. In order to do this, however, requires detailed knowledge of specific populations. Managers must know how recreational activities affect particular species, and at what intensities and when during the species' annual cycle such activities are harmful. Because different populations of the same species respond differently to the same type of stimulus, resource managers must tailor management approaches to individual populations. In addition to the variation between populations, there is also considerable within population variation in the responses of individuals to disturbances. Although it has not been attempted, managers could tailor management plans at the unit of individuals. For example, among a nesting population of bald eagles some individuals may tolerate much more disturbance than others. Accordingly, spatial and temporal restrictions could be tailored from nest to nest. This approach would be difficult to enforce and is perhaps unrealistic to expect people to understand.

Within the concept of coexistence mechanisms, there are four categories of restrictions which may be implemented: spatial, temporal, behavioral, and visual.

Coexistence mechanisms

Spatial: Spatial restrictions are perhaps the most common management technique used to control recreational disturbance. This is because they most closely resemble the original approach used to control harmful disturbance, that is, deny human access. The concept here is to spatially separate recreationists and wildlife. It can be done through at least two ways, closures and buffer zones.

Closure - Closures or refuges exclude recreationists from areas so wildlife can exist unmolested. Closures may be intentionally designed or unintentionally exist. In Denmark, 'game-pockets' are established where recreationists are prohibited and where roe deer seek shelter during orienteering events. In the United States, refuges may exist where game animals can retreat during the hunting season (Root et al. 1988). The National Park Service closed campgrounds near osprey nests once it was demonstrated that this activity was lowering reproductive success (Swenson 1979). It has been recommended that agencies withdraw critical bighorn sheep habitat from recreational use in areas where sheep show avoidance to humans (King and Workman 1986). Tuttle (1979) has suggested that critical bat caves used for hibernating and rearing young be closed to all human activity. In Sweden certain islands were established as nesting sanctuaries for Arctic loons (Gotmark et al. 1989). This action has played a critical role in the maintenance of a stable population as nesting success on unprotected islands was quite low. Waterfowl were able to use a London reservoir despite an intensification of sailing activities (Batten 1977). This use, however, depended on the existence of an area of the reservoir which was not accessible to the boats and hence acted as a refuge. The provision of temporary reserves on lakes used by both waterfowl and fishermen would allow

waterfowl to feed and roost unmolested (Bell and Austin 1985).

Finally, reserves may unintentionally exist where wildlife can escape from disturbing activities. Because of topography, tree-stand density, or lack of roads, Maine deer had access to areas where snowmobiles could not go (Richens and Lavigne 1978).

Buffer zones - Buffer zones are spatial areas where managers temporarily isolate wildlife from factors that would disrupt normal life-history processes. Closures and refuges differ from buffer zones in that the former are permanently set-aside, whereas, buffer zones are temporary. Because buffer zones are designed to allow wildlife to function in a normal state, they center around areas that are crucial to the survival and reproduction of wildlife. This would include sites such as feeding, breeding, roosting, and nursery areas. Jeppesen (1987a, b) determined that the flight distance of roe deer was noticeably shorter at night than during the day, therefore, spatial restrictions could be different during these two time periods. Although this might not be feasible in terms of enforcement and public awareness, temporal differences in spatial requirements should be kept in mind.

Buffer zones will differ for the same species depending upon the type of disturbance, the area being protected, the time of the year, and the type and magnitude of disturbance. Flushing responses and flight distances are usually used to determine the spatial distances necessary for buffer zones. It is important to note that a single buffer zone distance for a single species will not be adequate (e.g., Fraser et al. 1985, Gotmark et al. 1989). There is considerable variation between populations in their responses to the same type of disturbance. It is equally important to decide when establishing buffer zones what proportion of the population using an area will be protected. A buffer zone

of 200 m may protect 50% of a population, whereas, a buffer zone of 500 m may be necessary to protect an entire population (Stalmaster and Newman 1978, Stalmaster 1980, Knight and Knight 1984). In addition, there are temporal variations in flight distances within a population. Flocks of Brant geese flew, on average, at a distance of 211 m in September, but by October the distance had increased to 367 m (Madsen 1988). To protect this population from disturbance would require knowing the greatest distance at which individuals put to flight during the hunting season.

Variation in flushing response and flight distance among different populations has caused considerable frustration for natural resource managers who seek uniform regulations for species over wide areas. One apparent reason for this variability is the widely different environments that animal's experience. For example, an experiment in which some deer were harassed with an ORV and some were not resulted in sharp differences in flushing responses. The harassed deer were much more likely to flush to an ORV than the undisturbed ones (Yarmoloy et al. 1988). Likewise, white-fronted and bean geese decreased their flight distances from 500 to 200 m following a ban on shooting. One site may require wide buffer zone requirements because individuals in that population are heavily persecuted, whereas, a population that is not persecuted will require much narrower limits. Natural resource managers need to understand this intraspecific variation, feel comfortable in explaining its origin, and tailor management schemes to individual populations (Knight and Knight Skagen 1988).

Temporal: Temporal restrictions are often used to isolate wildlife and recreational disturbance and need only be in place when wildlife are using a critical resource (e.g., feeding, bathing, roosting, nesting). For example, in the Pacific Northwest wintering populations of bald eagles feed primarily in the

morning hours (Knight and Knight 1984, Skagen et al. 1991, Knight et al. 1991).

Temporal restrictions are necessary between 0800 and 1200 from October to March

to allow eagles to feed on salmon carrion (Stalmaster 1980). Likewise, Anthony

and Isaacs (1989) suggested that human activities be restricted from 1 January

to 31 August around bald eagle nests in Oregon. They further suggested that

these guidelines could be relaxed when nest sites are unoccupied or nesting

attempts fail early in the breeding season.   As with spatial constraints,

temporal restrictions must be tailored to the requirements of specific

populations, or even individuals.

There is abundant evidence (reviewed elsewhere in this report) that the

timing of disturbance is critical in understanding the impacts of that

disturbance. Spring and summer can be a critical time for desert bighorn sheep

in southeastern Utah. Ewes may either be pregnant or lactating and summer forage

is at its lowest nutrient levels (King and Workman 1986). Temporal restrictions

need to be in effect during these times to minimize unnecessary energy

expenditures. For colonially-nesting animals, disturbance during the egg-laying

and early incubation period may result in nest failure (e.g., Kury and Gochfeld

1975, Tremblay and Ellison 1979, Tuttle 1979, Bunnell et al. 1981, Safina and

Burger 1983); therefore, temporal restrictions need be in effect which protect

these colonies from disturbance during these sensitive time periods.

Temporal restrictions are traditionally thought off in times of weeks or

months but that need not always be the case. As an example, many ducks feed at

night, or dawn and dusk, so that daytime limitations are not always necessary

(Tuite et al. 1983, 1984). Likewise, Knight et al. (1991) studied a

scavenging guild in the Pacific Northwest in an area that had a two-day-a-week

sport fishing season; the river was virtually undisturbed the remainder of the

week. This temporal arrangement allowed for both recreational fishing and avian scavengers to obtain adequate food.

Other temporal variations exist which could be useful in developing management restrictions. Van der Zande et al. (1984) determined that weekend disturbance was far higher than weekday activities. Depending on the particular levels of disturbance and sensitivity of the species involved, temporal restrictions in certain situations may not be necessary on weekdays.

Behavioral: Although spatial and temporal restrictions on human activities are the most often used management techniques, alteration of human behavior is also a viable management approach. Because noise, speed, and type of recreation produce different responses in wildlife, aspects of these categories could be altered which would minimize the impacts of recreationists. For example, waterfowl are wary species and seek refuge from most forms of disturbance, particularly if they are associated with loud noise and rapid movement. If noise and movement could be lessened there would be an increased probability of coexistence. A paucity of information on how human behavior affects wildlife has kept the usefulness of this coexistence strategy from being used to its potential.

Visual: Many studies have noted that wildlife are much less reluctant to flush and flee when they are visually shielded from disturbance (e.g., Singer 1978, van der Zande et al. 1984, Vos et al. 1985, Singer and Beattie 1986, Jeppesen 1987a, b, Hamr 1988, McLellan and Shackleton 1989). For example, the response of white-tailed deer to snowmobilers was partially determined by whether animals were in areas of dense vegetative cover. Timber allowed deer to observe an approaching snowmobile without being exposed; in these cases they would remain standing rather than flee (Richens and Lavigne 1978). Likewise, mountain goats

were more successful at road crossings when they were shielded from humans by forest cover (Singer 1978). When roe deer were disturbed in Denmark, they would run into dense vegetative cover and remain there until the disturbance had passed (Jeppesen 1987a,b). This is an important principle as it allows for shorter spatial restrictions separating critical wildlife-use areas and disturbances. Visual buffer zones may also allow more recreational activity than areas without these screens (Root et al. 1988).

The importance of visual screening, however, is not always positive. Feeding bald eagles and other avian scavengers prefer to be far away from vegetation which may screen their vision from potential danger (Skagen et al. 1991). Geese in Scotland preferred to feed in large fields, regardless of whether food was more abundant there or not (Newton and Campbell 1973). It was suggested that geese felt more safe when they had greater open distances between themselves and potential threats. Pink-footed geese in Denmark avoided areas where vegetation or topography hindered their views (Madsen 1985).

Although the positive aspects of visual screening do not apply to birds that are feeding on the ground, perched birds will allow much closer approaches by humans when shielded by vegetation (Stalmaster and Newman 1978). Another component of visual screening deals with the juxtaposition of the animals, the location of the vegetation, and the location of potential danger. For example, when screening vegetation is near the source of disturbance (as opposed to near the animals), it may allow animals to use areas closer than usual to the disturbance (Batten 1977).

Design mechanism

Design of facilities in wild areas: To the degree that managers understand certain aspects of factors which disturb wildlife, they should be able to design

facilities (e.g., campsites, viewing areas) which decrease negative impacts on wildlife. As an example, because raptors and other cliff-nesting birds are more sensitive to disturbance from the top of the cliff than the bottom, overlooks could be designed which minimize potential conflicts (Hooper 1977). Campsites are often situated along riparian areas which may also be preferred nesting sites for birds that are susceptible to disturbance (e.g., Ream 1976, Swenson 1979). Campsites could be designed or placed in such a way as to insure spatial and visual restrictions are adequate to allow sensitive wildlife to exist. For example, these areas could be situated so patches or strips of vegetation lie between them and important wildlife habitat. Existing understory vegetation should be maintained in campsites and both horizontal and vertical heterogeneity should be enhanced. This would allow for greater species diversity as well as minimize overt effects of disturbance (Blakesley and Reese 1988).

RESEARCH NEEDS

That recreational activities disturb wildlife is both well appreciated yet poorly understood. What is understood is that wildlife flush and flee in response to disturbance, but what is not known are the processes whereby recreational disturbance affects wildlife. Recreational use of wildlands is popular and is expected to become more so, thereby leading to increased conflicts among recreationists and the goals of wildland managers. In order to develop effective management plans that will insure healthy wildlife populations, there will have to be a much better understanding of both direct and indirect impacts of recreational disturbance on wildlife. At present most studies are deficient in any number of ways: they may cover too short a time period, not have adequate controls or replications, be anecdotal in nature, or have too many potentially-confounding variables (Batten 1977, Cook 1980, van der Zande et al. 1984, Bell

and Austin 1985, King and Workman 1986, Anderson 1988, Knight and Knight Skagen 1988).

Although seldom done, research questions should be designed to examine short- and long-term effects, as well as direct or indirect effects. Short- and long-term effects incorporate the concept of both proximate and ultimate impacts on populations or communities as well as the idea of learning and change in gene frequencies. Direct effects are usually an animal's immediate response to disturbance while indirect effects involve potential additive or synergistic impacts.

Perhaps because behavioral data (e.g., flushing responses, flushing distances) are easily obtained, most studies have focused on overt behavioral responses. What has been neglected, however, are studies that examine physiological, genetic, and demographic impacts. Likewise, if populations are altered due to disturbance then research examining changes in community composition are needed (Robertson and Flood 1980).

Given the present state of our knowledge, there are gaps in our information which are readily apparent and that can be resolved only through well-designed experiments or descriptive studies. Because different recreational activities affect wildlife in disparate ways (e.g., Grubb and King 1991), we need to design comparative studies that assess how different types of disturbance affect wildlife. Likewise, since the magnitude and frequency of disturbance can alter wildlife responses, studies are necessary which measure threshold levels of these variables on wildlife.

The role of learning in shaping wildlife responses to disturbance is a field replete with dogma and in need of well-designed studies. Considering that data is subjected to external review before appearing in referred journals, it is

surprising how many unsubstantiated statements concerning habituation, avoidance, and attraction have appeared in scientific journals (see Stalmaster and Newman 1978, Knight and Knight 1984). At present, there are few adequate studies which have demonstrated any of these three types of learning responses in wild animal populations. There are none which have attempted to demonstrate all three experimentally.

Any study on learning would be incomplete without an understanding of the motivation or the decision-making process preceding the animal's response. Animals are capable of making complex contextual decisions (e.g., Orians 1981) and, in a given situation, they should be expected to weigh the many factors involved, their internal state and the external ecological circumstances, and act in a way that maximizes benefit and minimizes cost to themselves. Assuming that learning plays an important part in individual responses to disturbance, one can ask whether increased tolerance, avoidance, or attraction responses are adaptive or maladaptive. For example, if wildlife tolerate humans, how will mortality be affected if persecution increases? Likewise, if animals seek out humans because of some reward (e.g., food), how does this affect population size?

Although learning apparently plays a disproportionate role in influencing wildlife responses to disturbance, there is also a genetic component. Persecution over an extended period of time might result in altered gene frequencies which could predispose animals to react differently (e.g., Knight et al. 1989). Although studies of this nature are difficult learning issues should be addressed in the greater context of a species' genome.

An area of research requiring increased attention deals with the physiological effects of disturbance. A central question is whether individuals can compensate for the lost energy ingestion (i.e., foraging) or the increased

energy expenditure (i.e., fleeing) due to recreational disturbance (e.g., Stalmaster and Gessaman 1984). The energetic consequences of disturbance are often alluded to in studies but seldom are quantified (but see Stalmaster 1983). The potential additive or synergistic aspects of this topic also require study. For example, if animals are forced to redistribute to areas free from disturbance, does this increased density result in increased competition for essential resources? Many animals are food-limited; if disturbance is increasing the difficulty in obtaining adequate energy then it may have serious consequences for species persistence (e.g., Burger and Gochfeld 1991).

Another important research area involves understanding the impacts of frequency and magnitude of disturbance on wildlife. For example, does the passing of a single boat along a river cause as much disturbance as several boats together? How many times and at what intervals are animals disturbed before they alter their use of an important area? How do visible disturbances equate to disturbances which are strictly audible? How important is the timing of disturbance? Does disturbance during the breeding season have more serious repercussions than disturbance during a time of the year when food is scare and the climate is harsh? If studies find no significant impact of recreation on animals, is that because disturbance is unimportant or simply an effect of too low a dose (van der Zande et al. 1984, Anderson 1988)? Any study on frequency and magnitude of disturbance must take into consideration the importance of individual species differences. Species differ widely in their behavioral and physiological responses to similar stimuli, and generalizations extended from work on one species to another are risky at best (e.g., Cook 1980).

Assuming that disturbance causes animals to flee and that suitable habitat elsewhere is occupied, what happens to animals that abandon an area because of

disturbance? Is redistribution after disturbance adaptive? If an animal leaves an area to avoid being disturbed, is it able to resume its normal activities (e.g., foraging, breeding) elsewhere? Within a population of individuals, is there is a continuum of tolerance levels to disturbance so that individuals are able to distribute themselves according to levels of human activity and individual tolerance? Such redistribution may have negative repercussions, such as lowering access to food of less tolerant individuals, or contributing to overcrowding of individuals in some areas which in turn leads to increased aggression and lower fitness. Studies on redistribution should emphasize the need for spatial considerations. Ideally, studies on the effects of disturbance should be carried out on a regional basis, since it is important to know where individuals go following disturbance (Batten 1977). If recreational disturbance was heavy, but only in a limited area, then perhaps wildlife populations would be able to show adaptive redistribution. If disturbance was heavy and evenly distributed throughout a region, then redistribution would not be effective.

If recreational disturbance does alter animal populations, then one must assume this response may alter the dynamics of a wildlife community. Accordingly, research on community structuring and the role of recreational disturbance may yield some potentially important findings regarding the overall health of ecosystems (e.g., Skagen et al. 1991).

RESEARCH DESIGNS

As with any field of study, our understanding of the effects of recreationists on wildlife in wildlands is replete with dogma (Romesburg 1981). Van der Zande et al. (1984) have suggested this is because of the methodological complexity of the problem. In order to attribute cause-and-effect to patterns requires controlled experiments, and even then, is dependent on certain

assumptions. Fraser et al. (1985) and others (e.g., Anderson et al. 1987) have decried the continued emphasis of conducting observational studies with retrospective analyses in order to understand the effects of human activities on wildlife.

Because controlled experiments are not always possible, a researcher may resort to 'natural experiments.' By comparing the responses of species from two or more areas under different regimes of human activity, reasonable conclusions can be drawn. For example, Erwin (1980) studied colonial nesting waterbirds in two areas along the Atlantic seaboard that historically had different regimes of human disturbance. Likewise, Knight and Knight (1984) studied flushing responses and flight distances of wintering bald eagles on two adjacent rivers, one which had heavy boating activity while the other had none. This approach, though preferable to observational studies, still does not allow one to infer cause-and-effect relationships; there is no substitute for well-designed experiments.

The lack of systematic studies on recreational impacts on wildlife is surprising since it is not difficult to experimentally manipulate recreational activities (e.g., Yarmoloy et al. 1988, Skagen et al. 1991). For example, to understand the impacts of rock climbers on cliff-nesting wildlife would entail having researchers on cliffs at randomly-chosen times and at randomly-chosen locations. This would not be difficult as ropes could be affixed to cliffs which the researchers could use to move about on the cliff face. Likewise, to understand the affects of canoeing activity on nesting birds would require the researcher experimentally introducing canoeists into the study.

Three research strategies have been proposed that would be suitable for determining recreational impacts on wildlife (van der Zande et al. 1984). The first is sometimes called the 'laboratory approach.' This entails finding a

number of plots that differ only in the recreational variable of interest (e.g., type or frequency of the activity). Any differences found from such a study could then be attributed to the single variable which differed. An obvious difficulty with such a design is finding an adequate number of replicates which are identical in all aspects but for the variable of interest. A second approach can be called the 'randomization approach.' This entails randomly assigning plots to either treatment or control and does not require that all plots be identical. If there is an adequate sample size to minimize Type I and Type II errors, findings from this approach can be attributed to the variable of interest. The final strategy is called the 'multivariate or factorial approach.' Here one carefully picks plots that cover the full range of combinations of several variables. This approach allows one to examine both main effects as well as interactions of the variables of interest.

The importance of sample size, adequate controls and the avoidance of pseudoreplication are essential to enhance the reliability of research findings. The violation of any of these components of sound research will jeopardize the validity of research findings (Hurlbert 1984, Morrison 1988).

Likewise, research on recreational impacts needs to be carried out on the appropriate spatial and temporal scales. Studies that focus on the redistribution of wildlife in response to disturbance should include an area large enough to understand what happens to the individuals that do redistribute (e.g., Buehler et al. 1991). A study which does not include an adequate area runs the risk of its conclusions being in an improper spatial context (Wiens et al. 1986).

The duration of studies is also important (Tuite et al. 1983, Wiens 1984). As an example, studies which have addressed recreational impacts on nesting bald

eagles have usually used only one or two years of productivity data (McEwan and Hirth 1979, Fraser et al. 1985). Because of the potential year-to-year variability in nesting success as a result of factors other than human disturbance (e.g., prey availability, age of birds, weather), it is recommended that reproductive success for a number of years be used in lieu of one or two years (Anthony and Isaacs 1989).

Finally, a workable approach to conducting research on recreational impacts involves the scientist working in close cooperation with natural resource managers (MacNab 1983). Managers commonly manipulate habitats or populations to achieve some objective. These manipulations could be designed not only to achieve a specific goal, but also to increase our knowledge of how outdoor recreation affects wildlife. The manipulation by the natural resource manager would be considered the treatment. All that would be necessary for this to become an experiment would be the addition of a control. For example, a wildlife manager may establish spatial restrictions to allow a wildlife species to coexist with recreationists. If the manager measured the flushing responses and flight distances of individuals within the spatial boundaries, and similar responses of individuals in other spatial contexts, important information could be collected.

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Table 1. Classification scheme of Pomerantz et al. (1988) for recreational-use impacts on wildlife.

Category of impact	Description of impact
Direct mortality	Immediate, on-site death of an animal.
Indirect mortality	Eventual, untimely death of an animal caused by an event or agent that predisposed animal to death.
Lowered productivity	Reduced fecundity rate, nesting success, or reduced survival rate of young before dispersal from nest or or birth site.
Reduced use of refuge	Wildlife not using refuge as frequently or in the manner they normally would in the absence of visitor activity.
Reduced use of preferred habitat on refuge	Wildlife use is relegated to less suitable habitat on the refuge due to visitor activity.
Aberrant behavior or stress	Wildlife demonstrating unusual behavior or signs of stress that are likely to result in reduced reproductive or survival rates.

Table 2. Classification scheme for the effects of recreationists on wildlife[a].

Category of impact	Description of impact
Community change	Over time, either an increase or decrease in species diversity.
Population change	Over time, either an increase or decrease in population size.
Altered survival	Immediate, on-site death of an animal.
Altered productivity	Reduced fecundity rate, nesting success, or reduced survival rate of young before dispersal from nest or birth site.
Altered use of an area	Not using an area as frequently or in the manner they would in the absence of human activity.
Altered behavior	Demonstrating unusual behavior or signs of stress that are likely to result in increased energy expenditure, reduced reproductive or survival rates.

[a]Modified from Pomerantz et al. (1988).